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Morphology and Structure of Staminate Inflorescences and Flowers of *Leitneria floridana* (Simaroubaceae): Revisited

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Leitneria floridana, a dioecious shrub indigenous to North America, was recently transferred from its own family Leitneriaceae (usually placed in 'Amentiferae') to the family Simaroubaceae (Sapindales). Its staminate inflorescence is catkin-like, bearing 40–50 large bracts arranged in a 5/8 phyllotaxis on the axis. In each bract axil, a varying number of stamens (usually 10) are produced. They have been considered to represent a (one- to) three-flowered cymule instead of a single flower. In reviewing the limited evidence for the presence of the cymule and the revised familial position of the species, I re-examined the structure of the staminate inflorescences by analyzing serial microtome sections. The results confirmed that the staminate inflorescence of *Leitneria* is a reduced form of a thyrse consisting of many cymules, and that each cymule consists of one central and two lateral flowers (florets). Each flower has four stamens arranged in a cross-like configuration, in contrast to the previously considered diagonal configuration. One or more stamens, however, may be lacking in each flower, particularly in the lateral flowers, resulting in a varying number of stamens in the bract axil.

Key words: flower, inflorescence, *Leitneria*, Simaroubaceae

Leitneria floridana Chapm. (Florida corkwood) is a dioecious shrub found in low, wet areas in the southeastern and south–central United States (Channell & Wood 1962, Bogle 1997). The species has been long considered to be the sole member of the family Leitneriaceae, with uncertain affinities, placed within the orders Leitneriales (class Amentiferae) or Sapindales (Rutales) (for review of the taxonomic history see Tobe 2011, and references cited therein). Subsequent molecular analyses, however, have shown that *L. floridana* belongs in the Simaroubaceae of the Sapindales (Chase *et al.* 1993, Fernando *et al.* 1995, Gadek *et al.* 1996, Clayton *et al.* 2007).

Within Simaroubaceae, however, *Leitneria* is still distinctive for having erect catkin-like inflorescences. A staminate inflorescence has 40–50 large scale-like bracts spirally arranged on its axis and a varying number of stamens in the bract axil. Earlier publications have described the stamens located in each bract axil as a single flower (e.g., Chapman 1860, Oliver 1867–1871, Baillon 1877, van Tieghem & LeComte 1886, Engler 1894, Trelease 1895). Trelease (1895, p. 68) describes the staminate flowers to "consist simply of a whorl of about 10 short filaments a little dilated at base." Abbe & Earle (1940), however, on the basis of vascular anatomy and analogy with staminate partial inflorescences in the Coryleae of the Betulaceae ("Amentiferae"), proposed that each bract subtends a (one- to) three-flowered cymule, rather than a single flower. Each staminate flower consists of four stamens, which are diagonally arranged, of which one to three may be lacking (Abbe & Earle 1940). All subsequent publications (e.g., Channell & Wood 1962, Cronquist 1981, Takhtajan 2009, Clayton 2011) have adopted this interpretation.

Despite these hypotheses, substantial evidence for the presence of the three-flowered cymule in the bract axil has not been reported to date. To explain the three-flowered cymule, Abbe

& Earle (1940) and Abbe (1974) presented sketches of the cymules as well as three-dimensional figures of the vascular systems of the cymules and flowers reconstructed from serial microtome sections. Accepting and understanding the presence of a three-flowered cymule in the bract axil is difficult. In addition, the placement of *Leitneria* in the Simaroubaceae even suggests the possibility that the bract subtends a single flower (usually with 10 stamens) because the family often has 5-merous, (diplostemonous) flowers (e.g., Cronquist 1981, Takhtajan 2009, Clayton 2011).

To understand how the staminate inflorescence of *Leitneria* is constructed and, if the cymule forms in the bract axil, how individual flowers are constructed, I re-examined the inflorescence structure by using serial microtome sections, as examined by Abbe & Earle (1940). Eventually, I confirmed that the staminate inflorescence is a reduced thyrse, consisting of many laterally branched, three-flowered cymules (hereafter, the word cymule refers to the structure formed in the bract axil). The disposition of the stamens within individual flowers, however, differs from the previously drawn configuration of Abbe & Earle (1940) and Abbe (1974). This paper, using micrographs of serial microtome sections, provides evidence that the staminate inflorescence in *Leitneria* is composed of cymules and shows the exact structure of individual flowers.

Materials and Methods

Staminate inflorescences of *Leitneria floridana* were collected from trees cultivated at the Missouri Botanical Garden between March and April of 2000 and 2001 (voucher: U.S.A., Missouri, St. Louis City, Missouri Botanical Garden, cultivated, perhaps originated in Butler County MO. *W.G. D'Arcy 3653* [MO 2426777]). The inflorescences were fixed in FAA (five parts stock formalin/five parts glacial acetic acid/90 parts 50% ethanol). Two cymules with 10 stamens, along with the subtending bracts, were dehydrated through an ethanol series and then embedded in Technovit 7100 (Kulzer, Wehrheim, Germany) for microtoming. Serial resin sections cut at a thickness of 5–7 μm were stained with Heidenhain's hematoxylin and mounted in Entellan. Micrographs of the microtome sections were obtained using a digital camera (Olympus DP71) attached to an Olympus BX-51 microscope.

Results and Discussion

The staminate inflorescences are catkin-like and have large scale-like bracts spirally arranged on the axis (Fig. 1A, B). With regard to the arrangement of the bracts, two apparent sets of parastichies were observed: five in one direction, and eight in the other. The bracts are arranged in a typical 5/8 phyllotaxis.

Each bract has a mass of stamens in its axil (Fig. 1C). The number of stamens varies among the cymules. Earlier reports have described the number of stamens to range from 3 to 15 (e.g., Chapman 1860, van Tieghem & LeComte 1886, Trelease 1895, Abbe & Earle 1940). Examination of stamen number in one inflorescence showed a total of 41 cymules on the axis, with variation in stamen number ranging from 4 to 13 (Fig. 2). Of the 41 cymules, 16 had 10 stamens. Cymules with 10 stamens were most abundant. In contrast, 4 and 13 stamens were found in only one cymule each. A general pattern was observed where the cymules in the lower position of the inflorescence had less than 10 stamens. To confirm whether the 10 stamens represent 3 flowers, I traced the vascular systems in the basal part of the cymule (Fig. 1D–H).

At the level below the 10 stamens, the vascular system was composed of a bract trace located on the abaxial side and a vascular cylinder on the adaxial side (Fig. 1D). No anatomical signs of the presence of bracteoles in the microtome sections were observed. The bract trace extended in an upward direction (Fig. 1D–H), leading into the bract. On the other hand, the vascular cylinder diverged in an upward direction, generating three groups of vascular bundles, one in the center and two on the lateral (or tangential) sides (Fig. 1E). Each group upwardly leads to a certain number of discrete vascular bundles. Thus, at the level

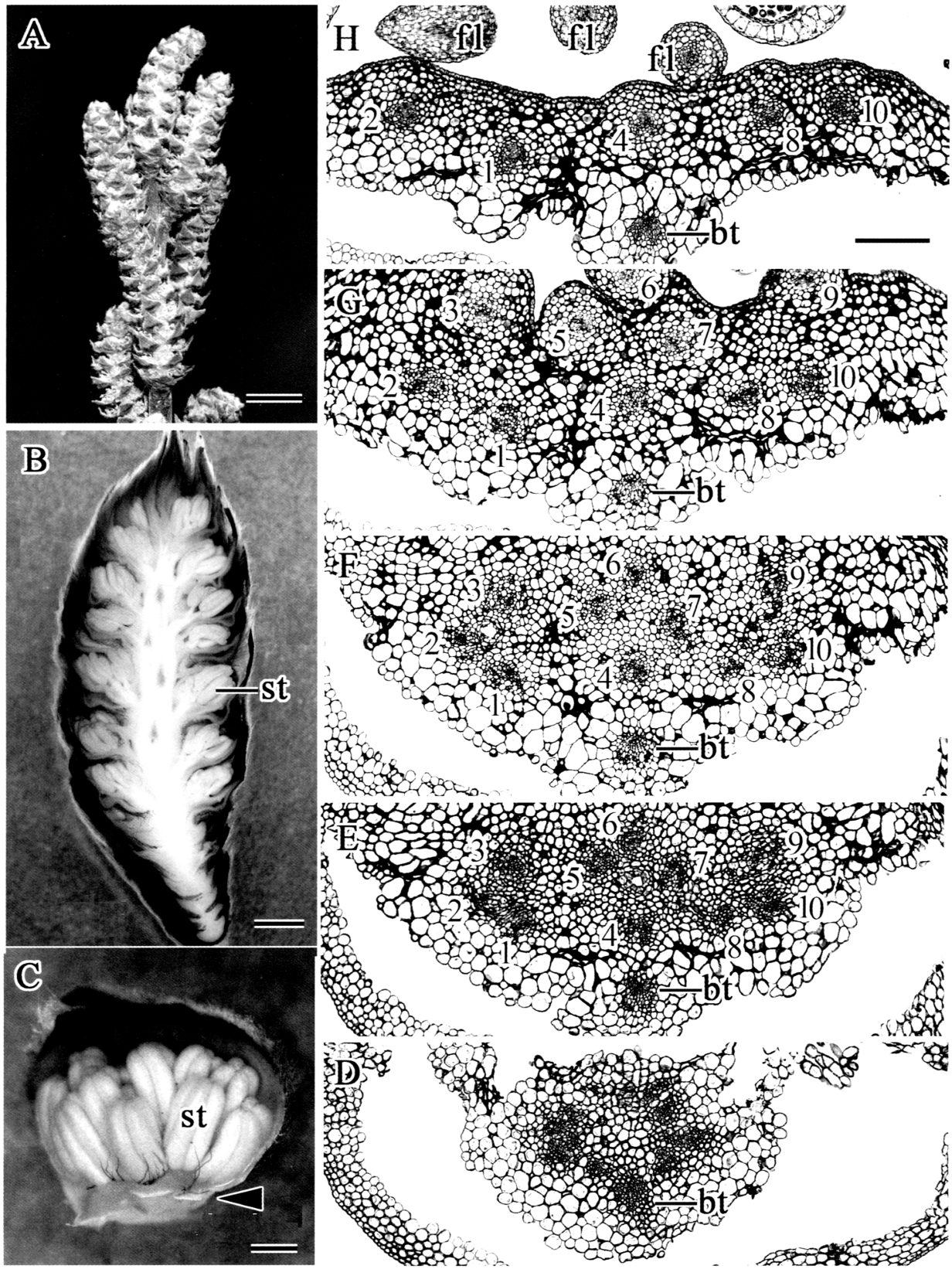

FIG. 1. Staminate inflorescences and cymules. A: Staminate inflorescences at anthesis. B: Half of a longitudinally dissected young staminate inflorescence. C: Eleven stamens (of a cymule) subtended by a single bract on inflorescence axis. Arrowhead indicates basal part of cymule that was sectioned in this study. D–H: Selected serial transverse sections of basal part of cymule showing course and disposition of 10 vascular bundles (traces) entering 10 stamens of cymule. bt, bract; fl, filament; st, stamen. Numerals 1–10 in E–H indicate vascular traces to 10 stamens. Scale bars = 2 mm in B, 700 μm in C, 200 μm in D–H.

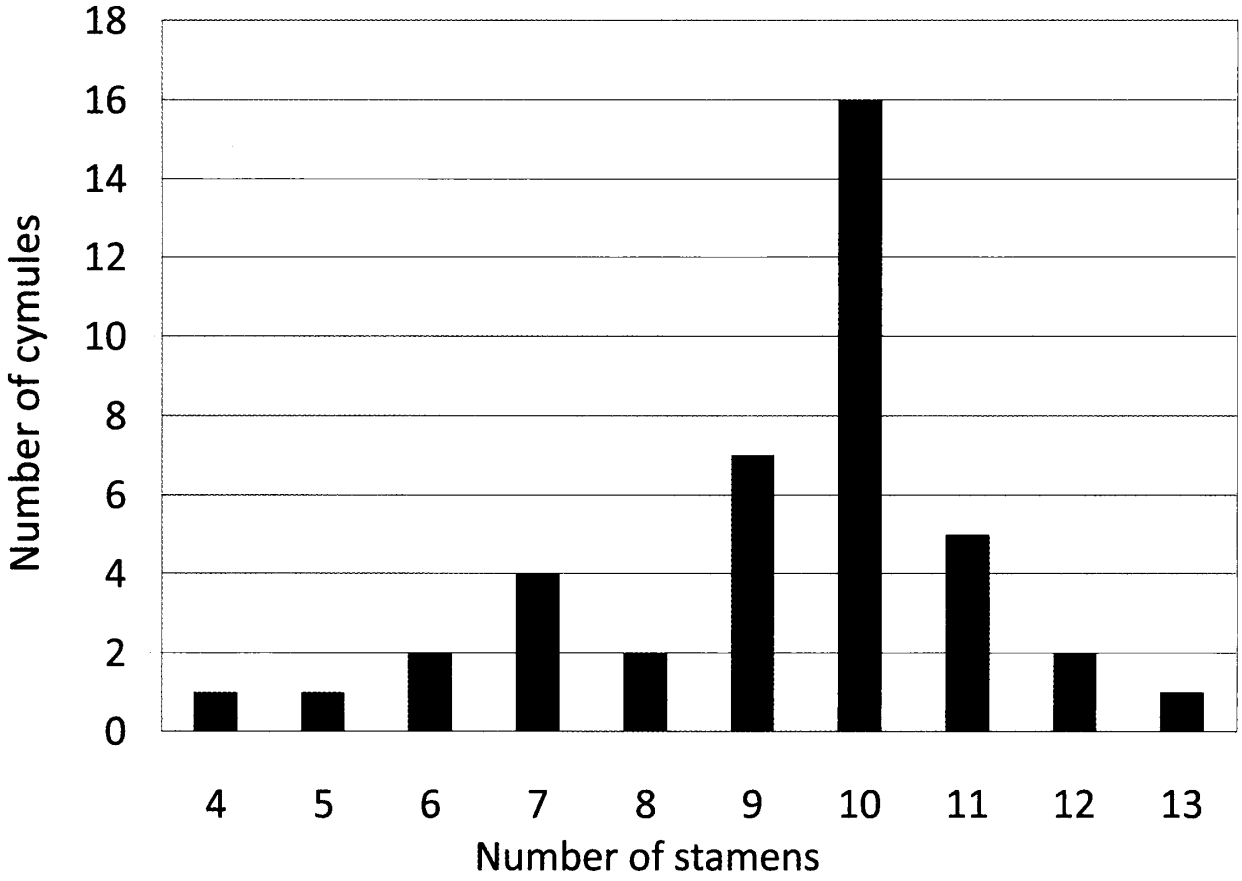

FIG. 2. Number of stamens (per cymule) observed in each bract axil of an inflorescence.

just below the stamen filaments (Fig. 1F), 10 vascular bundles were counted, four (numbered 4–7) in the center and three each (numbered 1–3 and 8–10) on both sides. The four vascular bundles in the center were arranged in a cross shape: two were radially positioned and two were tangential in relation to the primary inflorescence axis. On either side, two (laterally positioned in relation to the central flower) of the three vascular bundles were opposite each other, and the remaining one (radially positioned on the abaxial side) appeared to lack a counterpart. All 10 vascular bundles enter the filaments one by one as traces to the 10 stamens (Fig. 1G, H). Here we confirm that there are three small flowers: one central flower with four stamens, and two lateral flowers with three stamens.

Thus, the staminate inflorescence of *Leitneria* is a thyrse, bearing many lateral cymules, each of which consists of three flowers, as proposed by Abbe & Earle (1940). Each staminate flower consists of only stamens and lacks both pistils and tepals. The stamens are basically four in number as in the central flower. In cymules with 12 stamens, they are likely crucially distributed in both the central and lateral flowers (Fig. 3B), in contrast to the diagonal configuration (Fig. 3A) suggested by Abbe & Earle (1940) and Abbe (1974), but the flowers often lack one or more stamens. Chapman (1860), Trelease (1895), and Abbe & Earle (1940) described the bract as subtending 5 to 10 stamens, about 10 stamens, and 3 to 12 stamens, respectively. This study showed that most of the cymules (i.e., 38 of the 41 cymules) had fewer than 12 stamens, and that cymules with 10 stamens, in which one stamen each was lacking in the lateral flowers (Figs. 1F, 3C), were the most abundant (Fig. 2). Abbe & Earle (1940: Fig. 11, p. 179) considered cymules with only 3 stamens to consist of the central flower alone.

In this study, I observed a single cymule with 13 stamens (Fig. 2), and van Tieghem & LeComte (1886) observed a cymule with as many as 15 stamens. This deviation is not strange, because *Leitneria* is now placed as one of the derived genera in the Simaroubaceae, a family which often has 5-merous flowers (e.g., Cronquist 1981, Takhtajan 2009, Clayton 2011). *Leitneria* may also rarely produce 5-merous flowers. Although the anatomy of the flowers was not examined, it is likely that in cymule having 13 stamens, one (probably the central one) of the 3 flowers of a cymule had 5 stamens, while the other two had 4 stamens. Likewise, in cymules having 15 stamens, all 3 flowers of the cymule likely produced 5 stamens. If they were 5-merous, an additional stamen should be present in the adaxial position, as in *Ailanthus* and *Brucea* (unpublished data).

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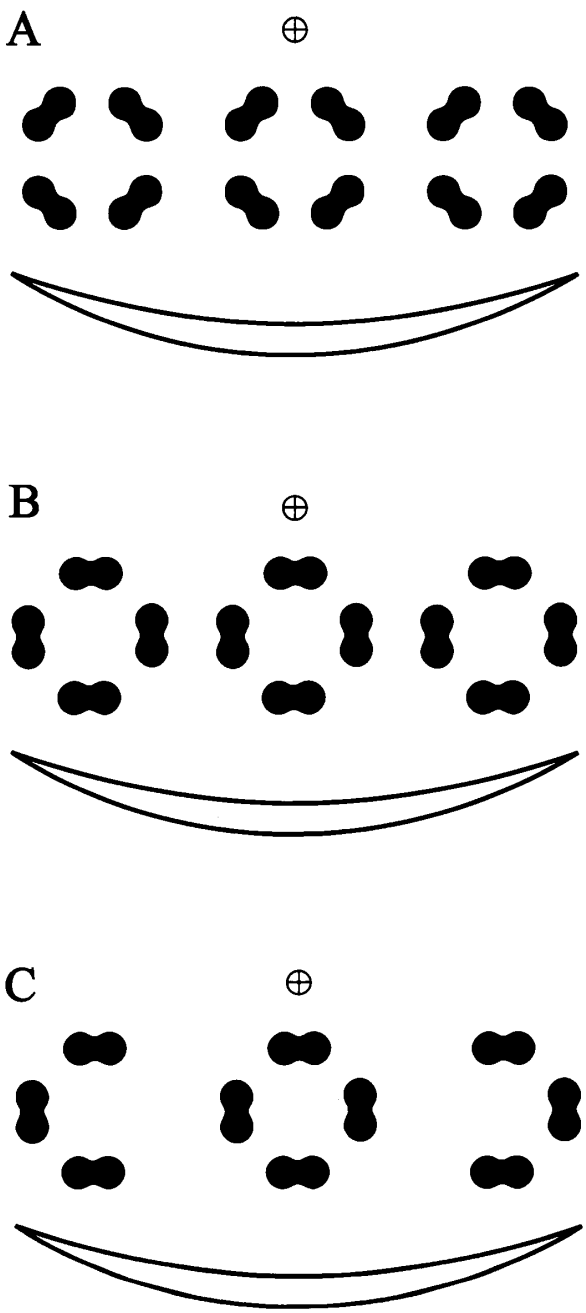

FIG. 3. Diagrams illustrating cymule with three staminate flowers. A: Cymule with 12 stamens, published by Abbe & Earle (1940). B: Cymule with 12 stamens, supposed on basis of present study. Single central and two lateral flowers with 4 stamens each. C: Cymule with 10 stamens, drawn on basis of present study, showing absence of one stamen in two lateral flowers.

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